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Researches on Potato-Virus Diseases in Montana

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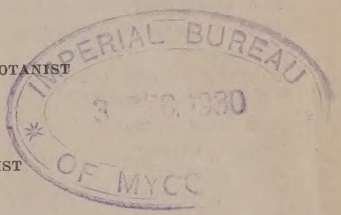

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Researches on Potato-Virus Diseases in Montana

INTRODUCTION

Profitable production of certified seed potatoes and of high yields of table-stock potatoes make it necessary to reduce the losses caused by virus diseases.

Much progress has been made in the study of these diseases in the world since 1913, when work on this subject was started at the Montana Agricultural Experiment Station.

This paper deals in particular with the results obtained since 1924 in finding better methods of diagnosis and control of these diseases.

Previous reports on this work were published by Whipple (89, 90), Morris and Young (52), Young and Morris (92, 94, 96), and Young (93, 95, 97). In these publications are illustrations and descriptions of many virus diseases.

REVIEW OF LITERATURE

Securing resistant varieties is a hopeful method of controlling viroses.* When leaves show a few mild or dim symptoms, are certain varieties resistant or tolerant, or are the symptoms masked? In Montana, Irish Cobbler and Netted Gem (Russet Burbank) potatoes appeared to be resistant to mild and crinkle mosaics, but both were severely injured by rugose mosaic. Netted Gem potatoes in Washington showed prominent symptoms of crinkle mosaic. Johnson (43) said that Bliss Triumph and Green Mountain were the most susceptible, and Rural New Yorker was the most resistant, of the varieties which he used. This statement agrees essentially with observations in Montana. Nishimura (58) said that *Physalis alkekengi* is a masked carrier of the tobacco-mosaic virus. Johnson (42) produced mottling in tobacco by inoculating with extract from apparently healthy potatoes. Fernow (27) suggested that the potatoes are masked carriers of the so-called "healthy-potato

*"Virosis" is a useful new word meaning virus disease, proposed by Dr. L. R. Jones at Lincoln, Nebr., on Dec. 28, 1925.

virus," which becomes evident when transmitted to tobacco and some other hosts.

Yellow dwarf, described by Barrus and Chupp (6), and streak (unmottled), described by Orton (59), have not been identified in Montana.

Blodgett (10) is one of the authors who described tobacco mosaic in potatoes. Severin (72) described curly top of potatoes. Fernow (27) and Elmer (24) made many interspecific transmissions of virus diseases. These articles show the need for identifying the viruses that cause the various diseases. Johnson (43, 44) classified several viruses; this valuable work shows relationships between some viroses, and needs to be extended to many others.

A large amount of experimental work has shown that viruses cause most of the diseases that were called degeneration, running-out, senility, and physiological diseases. Schultz (69) and Schultz and Folsom (68) gave this widely accepted explanation of degeneration of potatoes. Hence, a variety of potatoes should remain profitable as long as its seed stocks contain only low percentages of diseases, and it meets cultural and market needs.

Some abnormalities such as giant hill, calico, and curly flavescence may be called genetic abnormalities instead of virus diseases until some one demonstrates that they can be transmitted from diseased to healthy potatoes.

Physiological disturbances such as hollow heart, black heart, sunburn, frost necrosis, and enlarged lenticels belong in categories different from the foregoing diseases.

Schultz and Folsom (68, 69, 70), gave excellent descriptions of many potato viroses, and did much to standardize their nomenclature in the United States. Barrus and Chupp (7) gave popular descriptions of many viroses. McKinley (50) and Rivers (62, 63) compiled much information about the virus diseases of plants and animals.

Davidson (20) and Atanasoff (5) gave extensive reviews of European literature on virus diseases of potatoes, showing that some of the most useful knowledge about them is a hundred years old or older.

Brown (12) stated that Parmentier mentioned degeneration of potatoes in 1786.

Davis (22) conducted physiological experiments on infectious chlorosis of plants. Those transmitted by grafting can be called virus diseases. Lantz (47) cited many publications dealing with non-parasitic diseases, which then included viroses. Black (9) described a peculiar tumor-like abnormality on the bases of potato stems.

Arthur (3) and Holmes (37) used a promising method in studying viroses with ultra-violet light.

Smith (74) secured valuable information about insect vectors, stating that insects like aphids are best adapted to transmit viruses because they inoculate phloems without causing great physiological disturbances in the host tissues.

Murphy and McKay (50) stated that decaying of mother tubers destroys the continuity between stems borne on the same tuber. Hence, field infection of only one stem of a hill will not affect all of the tubers of the hill.

Hoggan (36) reviewed reports and gave new information about intracellular bodies in solanaceous plants. Eckerson (23), Nelson (56), and Sorokin (78) described organisms in chloroplasts. Perhaps these are visible forms of viruses.

Swezy and Severin (80) gave evidence that an ultramicroscopic organism has a visible stage.

Likhite (48) summarized previous work and concluded that certain intracellular bodies caused tobacco mosaic. He gave them a new binomial name. It is hoped that he will present evidence proving the causal relationship of Vacuolarium.

Two older articles are worthy of reconsideration. Eriksson (25) described mycoplasm. Loehnis and Smith (49) described a symplastic phase in the life cycle of bacteria, and stated that some bacterial gonidia are filterable. Are viruses phases, lacking cell walls or definite morphological shapes, in the life cycles of definite organisms having recognizable shapes or cell walls in other phases? Accumulated evidence points toward a positive answer to this question. Cell walls and definite morphological shapes are not fundamental attributes of life.

Alexander and Bridges (1) suggested autocatalysis as the way in which life originated. This hypothesis gives an interesting concept of a virus.

The studies of the natures and controls of virus diseases have practical and much permanent value.

PRIMARY AND SECONDARY SYMPTOMS

The terms "primary symptoms" and "secondary symptoms" are used here according to the definitions: (a) When infection (especially of leaves) and symptoms occur in the same generation of a plant not previously having the disease, the symptoms are called *primary*. (b) *Secondary* symptoms are those which appear in plants grown from diseased tubers produced by diseased parents. This is similar to seed transmission of mosaic in beans. These definitions are essentially like those given by Hungerford and Dana (41). Time of appearance of symptoms is the main basis for these definitions because the primary and secondary types of symptoms often intergrade.

Secondary symptoms of rugose mosaic developed in many new leaves of potatoes having primary symptoms. Tubers inoculated with witches' broom by core grafts produced vines with primary symptoms, but tubers inoculated with rugose mosaic by core grafts produced vines with the secondary types of symptoms. Murphy and McKay (55) state that, "Infection of the sprouts of unplanted tubers results in the development of secondary leaf roll very early in the season, usually without the intervention of the primary stage * * *." Hence, infecting tubers with leaf roll or rugose mosaic has effects similar to infecting their parent plants.

METHODS OF TRANSMITTING VIROSES

Core grafts: Normal tubers for inoculation were cut into two to eight seed pieces weighing 50 to 100 grams each. One or more seed pieces from each tuber were planted as checks. In the tables these checks are described as "healthy checks from same tubers."

Using nickel-plated cork borers, cores 1 to 5 cm. long and 5 to 10 mm. in diameter were removed. When possible, holes in the stock seed pieces were made parallel to the vascular rings with cork borers one or two sizes smaller than those used in removing the scion cores. In grafting similar varieties, the bark was cut from the ends of the scion cores so that it was

certain that the cores bore no buds. Buds were left on the cores of some varieties that were unlike the stock seed pieces. When grafted tubers were stored in the refrigerator for ten or more days before planting, high percentages of the cores (scions) became attached to surrounding tissues and remained solid. The seed pieces were planted in a sand bed or field. Some seed pieces were kept in a damp chamber for a day after cutting to aid in callusing, but rotting was not diminished by this method. Potatoes in sand beds were transplanted to pots 12 to 18 cm. wide as soon as the sprouts were 2 to 7 cm. long. Numbers written with India ink on the seed pieces when they were grafted were usually readable when they were transplanted a month later. Many of such numbers also remained legible for a month or longer in fields.

This method of core-grafting tubers is essentially the same as that described by Murphy and McKay (53, 54) and Goss (33). The cutting knives and nickel plated cork borers were disinfected with 5 per cent formaldehyde and then rinsed with water before changing to different scion and stock tubers. The hands were disinfected frequently with laundry soap. The table was washed with 1 per cent Uspulun before laying fresh groups of cut seed pieces upon it. The greenhouse was frequently fumigated with hydrocyanic acid gas, and plants were sprayed with strong nicotine sulphate or emulsions of petroleum oils to control aphids and other insects. Hence, there was very little danger of unintentional transfer of potato viruses.

Leaf mutilation inoculations: The method of making leaf-mutilation inoculations was similar to that used by Schultz and Folsom (70). Stems and leaves of diseased potato plants were macerated in an autoclaved food grinder and placed in sterile dishes. The hands were disinfected with laundry soap before inoculating new plants. Care was taken to prevent contamination of the inoculum from the possible presence of a virus in inoculated plants. Each inoculation was made by rubbing and pressing bits of freshly macerated inoculum against the leaves until the latter were ruptured. The macerated tissues were left on the injured spots. Plants were 8 to 20 cm. tall and growing vigorously at the time of inoculation. In many cases they were reinoculated two or three times at intervals of three to seven

days. Plants usually were kept damp for 10 to 20 hours after inoculation.

Stem grafts: Three methods of grafting herbaceous stems were used. (a) Cleft grafts were made by inserting scions into clefts made in the stocks. (b) Whip grafts were made by inserting scions into slits made in the sides of the stock stems. (c) Inarch grafts were made by slicing off the outer layers of cells on one side of each of two stems and binding the cut surfaces of the stems together while the roots of both plants remained undisturbed in the soil.

All grafts were tightly wrapped with heavy string and painted with melted grafting wax. Paraffine is a useful substitute. The few drops of grafting wax that fell on the leaves slowly caused unimportant leaf spots. High humidity was maintained in the room only while the grafts were being made. Grafts were not unwrapped for one to two months, so growth kept the cut surfaces in close contact. The resulting constrictions of the stems did not appear to be injurious.

Aphids: Non-viruliferous aphids were colonized on caged normal potato vines in the greenhouse.

For inoculations, such aphids were colonized on diseased potatoes for a few weeks. Leaves bearing viruliferous aphids were excised and placed upside down on the leaves of young, normal potato plants. Usually three transfers of aphids were made in this way at weekly intervals. Inoculated plants were grown to maturity and their progeny tubers were tested. Greenhouse temperatures usually varied around 15° to 25° C.

Cages: In the field, potatoes were grown in cloth cages to protect them from insect vectors. Mottling of mosaic was more prominent in mosaic plants in cages than in uncaged plants because the air in the cages was cooler than the air outside. Burns (13) described the environment of caged plants.

Other methods of handling potato plants: Potatoes were grown in the laboratory, in the greenhouse, and in three fields. One field was irrigated, one received only a little subirrigation water, and the other received no irrigation water. Potato tubers were stored in a refrigerator and in good potato cellars.

Pressed specimens of leaves mottled by mosaic were kept in the herbarium where the mottling remained visible for years

after the leaves turned brown. Mottling in specimens was well preserved by the copper acetate method.

The tops of maturing potato plants often were cut off to hasten the appearance of viroses symptoms. Such symptoms appeared in new leaves that developed after the excision of the tops in many cases.

ISOLATED SEED PLOTS FOR SEED POTATOES

Chapple (16) in 1795 grew potatoes in special plots which he isolated and rogued to control curl. Many recent publications have recommended these valuable methods, yet they are used by too few of the growers of certified seed potatoes. Figures given by Anderson and Miles (2) show the result of this neglect. Certification rules should require that the seed potatoes for the main field be grown in isolated, specially rogued seed plots. Webb (85) in 1792 planted many selections of potatoes in hotbeds, and selected for field planting those with minimum amounts of curl. He described this method in 1785. Nicol (57) in 1802 said that seed potatoes from outside sources had little value unless they were healthy. Davidson (21) described the rejuvenation of the Champion potato. Whipple (90) in 1917 recommended rogued seed plots in Montana.

Normal potatoes for checks and inoculations were grown at Bozeman for three years in a plot 100 m. from other potatoes. Some selections were tuber indexed in the greenhouse. Very little roguing was needed each year to keep visible virus diseases out of these plots. Expensive methods of controlling insect vectors are often justified in special seed plots.

Potato plots were often separated by planting wheat or sunflowers between them. Such plants may decrease the spread of aphids to different plots.

TUBER INDEXING TO IMPROVE STOCKS OF SEED POTATOES

Tuber indexing in greenhouses, as described by Blodgett and Fernow (11), is a valuable method of eliminating from foundation seed stocks, diseases with dim symptoms that are more effectively recognized in the greenhouse than in the field. Indexing in greenhouses aids especially with super-mild mosaic and mild mosaic. It has little value with giant hill and mild

forms of spindle tuber which are not readily recognized. Diseases with very prominent symptoms, like witches' broom, rugose mosaic, and severe forms of spindle tuber, are readily eliminated to a practical degree in isolated tuber-unit plots.

Obviously, tuber indexing is worth its cost only in cases where the benefited seed stock is sufficiently well protected from infection by disease during subsequent years. Most growers have not yet been sufficiently careful to justify the cost of tuber indexing. Valuable seed stocks need occasional indexing to lower the percentage of disease in them. The length of the interval depends upon the rapidity with which the percentage of disease increases in them.

TRANSMISSION AND SYMPTOMS OF RUGOSE MOSAIC

Aphids were unusually abundant in fields at Bozeman in August and September, 1926.* That year, potatoes with rugose mosaic were planted near other potatoes in an experimental plot. The aphids spread the virus of rugose mosaic so that primary symptoms appeared in about 100 potato plants. Eighty-five tubers from 12 of these infected plants were tested in the greenhouse. These tests, recorded in Table 1,† showed that aphids had transmitted the virus causing the primary symptoms in the parent vines.

The characteristic primary symptoms were browning and blackening of veins near the points of inoculation; brown streaks visible in the surface of the petioles and stems; necrotic leaf spots; and progressive dying of parts of leaflets, entire leaflets, compound leaves, and entire stems. Discolored veins were most prominent and common in the lower sides of leaflets. Some vines produced new leaves that were rugose and mottled, but these secondary-type symptoms usually appeared only in the progeny of infected vines.

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*Dr. J. R. Parker, entomologist, found three species of aphids in potato fields at Bozeman. These species were *Macrosiphum solanifolii* Ashm., *Myzus pseudosolani* Theo., and *Myzus persicae* Sulz., as determined by Dr. Edith Patch of the Maine Experiment Station. *M. solanifolii* usually was the most abundant.

†All tables may be found on pages 45 to 51.

Willowy, spindly tops appeared as a late season symptom of rugose and crinkle mosaics in separate plants in the greenhouse. New, spindly stems developed in the tops of old plants (Fig. 1).

Fig. 1.—Willowy growth. A late-season symptom of rugose mosaic in greenhouses. American Wonder variety. Seed piece infected by core graft from Irish Cobbler potato with rugose mosaic. Stem supported by a glass rod in photograph.

Table 2 and Figure 2 show the results of inoculations made to transmit mosaic diseases. Primary symptoms of rugose mosaic followed leaf-mutilation inoculations with the causal virus. These symptoms were very similar to those resulting from aphid transmission of this virus in the field.

As shown in Figure 2, 60.8 per cent of the 102 inoculations with the rugose-mosaic virus in a selection of Irish Cobbler potatoes transmitted the disease. The incubation period was usually 21 to 40 days. Schultz and Folsom (68) gave the incubation periods of many viroses.

Rugose mosaic in a selection of Bliss Triumph potatoes was transmitted in 52 per cent of the 25 inoculations made with it (Table 2 and Fig. 2). Core-graft inoculations with rugose mosaic usually caused the secondary type of symptoms. Apparently, introducing the virus in this way had the same effect as inoculum reaching the tubers from the parent vines.

Secondary symptoms of rugose mosaic in potatoes were: prominent, dim, or no mottling; prominent rugosity, ruffling and dwarfing of leaflets; necrotic leaf spots; premature dropping of lower leaves; brown streaking of stems, and upright, narrow, rigid vines. Below 25° C., rugose mosaic caused large, prominent, mottled spots.

The symptoms of rugose mosaic were very severe in 3 Bliss Triumph and 3 Green Mountain plants. They reached heights of only 5 to 15 cm., and had dwarfed, curled, rugose, abnormally hairy leaves. The lower leaves dropped and the plants died within a few weeks, before producing tubers. The leaves showed no mottling, but related plants in the same selections were mottled.

Necrotic leaf spots caused by rugose mosaic were sectioned. Affected parts of the leaves showed collapsed, dead cells (Fig. 3). There were many spherical or irregular bodies in the dead cells. These bodies stained red with saffranin in Flemming's triple stain. Most of them were smaller and less definite than the intracellular bodies caused by leaf roll (Pl. 1, B).

Necrotic, brown to black leaf spots, usually 1 to 3 mm. in diameter, are a common symptom of rugose mosaic, especially following inoculations. Many of the leaf spots have dark-green borders. They fuse, and kill leaflets.

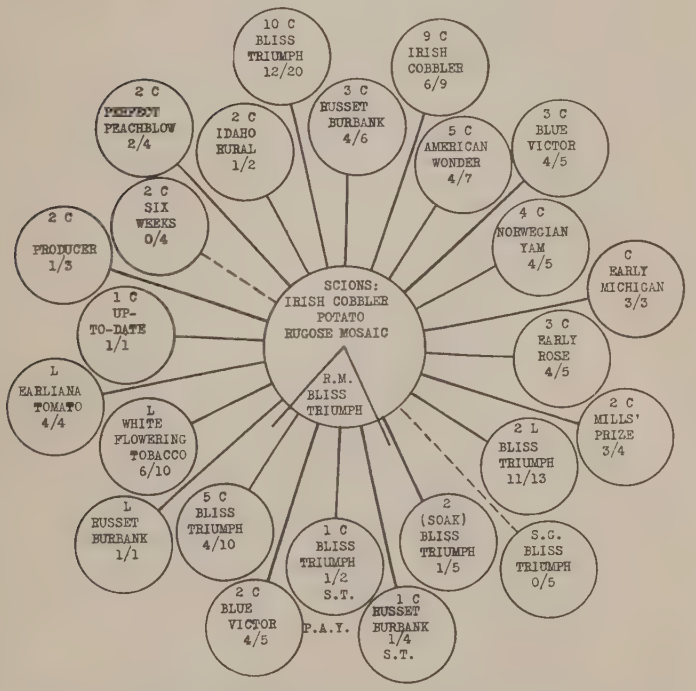

Fig. 2.—Chart showing the transmission of the rugose-mosaic virus to many varieties of potatoes, and also to tomatoes and tobacco. The central circle shows that Irish Cobbler and Bliss Triumph potatoes with rugose mosaic were used as sources of material for tuber cores, stems for grafting, and leaves for maceration in inoculating the plants described in the small circles. The varieties of the potatoes inoculated are named in the small circles. The numbers and key letters in these circles signify as follows: The number at the top of the circle refers to the number of healthy checks from the same tubers as the inoculated plants. The letters following such numbers mean: C—core grafts of the seed pieces; L—leaf-mutilation inoculations; S. G.—inarch-stem grafts. In the fraction in the bottom of the circle, the denominator refers to the number of inoculated plants and the numerator refers to the number of infected plants. Solid lines connecting the large and small circles mean that infections occurred; broken lines mean that infection did not occur.

Very severe symptoms appeared when the rugose-mosaic virus was transmitted from a selection of Irish Cobbler potatoes by leaf-mutilation inoculations. Inoculated potatoes soon showed severe primary symptoms ending in premature death.

Possibly most potatoes become rather tolerant to this virus in the generations succeeding the one in which infection occurred, so that the necrotic symptoms are less common and severe in tuber-perpetuated plants than in plants recently infected through leaves.

Thrips and mealy bugs did not transmit rugose mosaic in any of the many experiments.

Macerated potato leaves with rugose mosaic were diluted with 100 parts of distilled water, and freshly cut seed pieces were soaked for ½ to 2 hours in this liquid. In one case a plant from one of the soaked seed pieces developed symptoms of rugose mosaic. All other inoculations of this kind failed, including those with crinkle mosaic (Table 2). The freshly cut surfaces of other seed pieces were smeared with macerated, mosaic-diseased leaves and kept damp for a few hours afterwards. All of these seed pieces produced healthy plants (Table 2).

As shown in Figure 2, rugose mosaic in Irish Cobbler potato leaves was transmitted by leaf mutilations to tomatoes and tobacco, in which it caused mottling.

Krantz and Bisby (46), Schultz and Folsom (68, 70), and Quanjer (60) are among those who have described transmission experiments. Para-crinkle (Salaman and LePelley, 65) and Crinkle A (Salaman, 64) appear to belong in the group of diseases containing rugose mosaic.

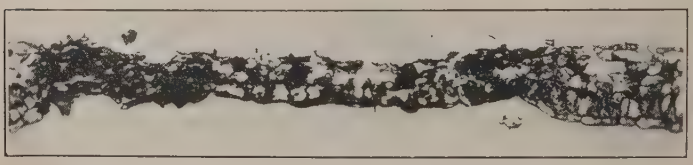

Fig. 3.—Photomicrograph of a section of a Bliss Triumph potato leaf showing a necrotic leaf spot as a primary symptom of rugose mosaic. Leaf-mutilation inoculation with the virus in an Irish Cobbler potato vine. ×73.

SYMPTOMS CAUSED BY NON-VIRULIFEROUS APHIDS

Aphids were numerous on Green Mountain potatoes in one cage in the field in August and September, 1926. Some of the leaves had browned veins strongly suggesting rugose mosaic, which was common then in uncaged plants, so 4 tubers from this plant were grown in the greenhouse. None of them produced plants with rugose mosaic, so the browning of the veins of the parent leaves was probably due to the feeding of non-viruliferous aphids. Presumably there had been enough time for a virus to reach the tubers. *Macrosiphum solanifolii* Ashm. (*Illinoia solanifolii* Ashm.) caused brown dots and general browning of veins when many non-viruliferous individuals fed upon normal Bliss Triumph potatoes in the greenhouse. These symptoms resembled the primary symptoms of rugose mosaic. Houser, Guyton and Lowry (38) illustrated leaf curling and killing of potatoes by this insect.

Heavy infestations of *Myzus persicae* Sulz. (non-viruliferous) were grown on normal potatoes in the greenhouse in several series. The leaflets were severely dwarfed and curled, and the tops were dwarfed and spindling as symptoms of the injury caused by the aphids.

Fenton and Hartzell (26) and Smith (74) described symptoms caused by the toxic saliva injected by insects.

HOPPER BURN AND TIP BURN

There is considerable evidence that hopper burn is not caused by a virus. It is not tuber perpetuated. Fenton and Hartzell (26) and Chupp (17) stated that hopper burn is caused by a species of leaf hoppers (*Empoasca mali* Le B.). Fenton and Hartzell (26) said that hopper burn was very destructive, while tip burn was neither abundant nor very destructive in Iowa. Since these diseases have been confused, these conditions may apply to other regions.

Tip burn appears to be a physiological abnormality mainly caused by hot sunshine and drying winds (Chupp, 17). Burns (13) made physiological studies concerning tip burn.

Early symptoms of hopper burn can be confused with the primary symptoms of rugose mosaic, so it is important that care be used in distinguishing them because the value of the crop for seed is concerned.

Smith (74) stated that leaf hoppers, aphids, and tarnished plant bugs inject toxic saliva into leaves which later show dead cells near injured places. He and Fenton and Hartzell (26) are among those who favor the theory that the saliva injected by leaf hoppers causes hopper burn.

Hopper burn does much damage in some parts of Montana, and is more serious in regions more salubrious for the causal leaf hoppers.

UNLIKENESS OF VIROSES

The transmission of different viruses to potatoes already affected with one virus is a valuable method of showing that some viruses are distinct from others. As shown in Table 3, the rugose-mosaic virus in Bliss Triumph and Irish Cobbler potatoes was transmitted to potatoes having mild mosaic, producing primary symptoms of rugose mosaic in them. These results support the evidence drawn from the differences in symptoms and virulence, that the viruses causing rugose and mild mosaic are different.

Rugose mosaic was transmitted to potatoes having leaf rolling mosaic, producing the symptoms of vascular streaking and premature death in them. Vascular streaking is a symptom only of rugose mosaic in the greenhouse here. This supports the evidence that these viroses are distinct.

Also, rugose mosaic was transferred by a core graft to a potato with spindle tuber, which is further evidence of their unlikeness. Other potatoes having both of these viroses exhibited symptoms of curly dwarf.

Leaf-mutilation inoculations were made with the virulent virus of rugose mosaic in Irish Cobbler potatoes, in an attempt to produce primary symptoms of rugose mosaic in potatoes already showing the secondary symptoms of this disease. None of the inoculated plants developed any new symptoms that would distinguish them from the checks (Table 3). This is evidence that the primary and secondary types of symptoms are caused by the same virus.

GRAFTING HEALTHY TUBERS WITH HEALTHY CORES

Forty-five normal seed pieces of the Sharples strain of Bliss Triumph potatoes were core grafted with scions from

healthy tubers of this variety in an attempt to detect differences between the early and late-maturing forms. Cores from the tubers of the early-maturing strain were placed in the seed pieces of the late-maturing strain, and vice versa. These grafted seed pieces, and 45 checks from the same tubers, produced plants which grew and remained normal in the greenhouse for 84 days. They did not differentiate the two strains. However, they were valuable checks on core-graft inoculations. Besides these check grafts, 4 Bliss Triumph seed pieces were core grafted with scions from Irish Cobbler and Netted Gem tubers, and 3 Netted Gem and 2 Irish Cobbler seed pieces were core grafted with scions from healthy Bliss Triumph tubers. All plants from them remained normal, so they constituted checks on the tuber grafts with scions containing viruses.

VIROSES FROM MAINE

In 1926, Dr. E. S. Schultz kindly supplied Green Mountain tubers containing the following viroses: mild mosaic, leaf rolling mosaic, crinkle mosaic, rugose mosaic, leaf roll, and spindle tuber. When grown in the field at Bozeman, these tubers produced plants having symptoms agreeing with those described for these different viroses by Schultz and Folsom (68, 70). The four kinds of mosaic were distinguishable.

LEAF ROLLING MOSAIC

Leaf rolling mosaic was transmitted from Green Mountain to Bliss Triumph and Netted Gem potatoes in the greenhouse (Table 2).

CRINKLE MOSAIC

Mottling and ruffling of leaflets, chlorosis and dwarfing of vines, and reduced yields are the main symptoms of crinkle mosaic. The mottled spots often are 5 mm. wide. Vascular streaking is a less common symptom, as it has not been seen in Montana. Table 9 shows reductions in yields. Table 2 shows transmission experiments.

Crinkle mosaic intergrades with the common form of mild mosaic which also mottles and ruffles the leaflets. Crinkle mosaic is distinctly unlike rugose mosaic when it intergrades

with mild mosaic. However, severe cases of crinkle mosaic resemble rugose mosaic.

MILD MOSAIC

Ordinary mild mosaic in Green Mountain, Idaho Rural, and Bliss Triumph potatoes shows ruffling and conspicuous mottling as distinctive symptoms. In many cases the vines are dwarfed little or not at all. Mild mosaic was transmitted 14 times in 59 trials (Table 2). It reduced the yield 23.1 per cent in Idaho Rural potatoes (Table 10).

SUPER-MILD MOSAIC

A form of mosaic, having dim and sometimes prominent mottling as the only observed leaf symptom, was encountered commonly in Bliss Triumph, Netted Gem, and Irish Cobbler potatoes. The leaves were normally smooth. The mottling was readily seen in index plants in the greenhouse. Close examination sometimes revealed the dim mottling in Netted Gem potato leaves in fields. This symptom was commonly masked in fields, so affected plants often passed as healthy. This form of mosaic was obviously unlike ordinary (ruffled) mild mosaic in symptoms, so for convenience it has been called super-mild mosaic during the last few years. Proof is lacking that these diseases are caused by different viruses. It was transmitted 5 times in 14 trials with Netted Gem potatoes (Table 2). It reduced yields 19.1 per cent (Table 10).

TYPES OF MOTTLING NOT CAUSED BY MOSAIC

Some normal Netted Gem potatoes in the greenhouse showed many hypophyllous intumescences which caused epiphyllous mottling. These were symptoms of a physiological abnormality instead of a disease.

Young Bliss Triumph potatoes in a greenhouse showed browning of hair and epidermal cells in some epiphyllous chlorotic spots. These chlorotic leaf spots resembled mottling caused by super-mild mosaic. Possibly not mosaic but light focused by drops of water caused these enigmatical chlorotic spots.

CURLY FLAVESCENCE*

A peculiar abnormality appeared in a field of Bliss Triumph potatoes at Bozeman in 1927. The symptoms clearly distinguished it from previously known abnormalities of potatoes. The characteristic symptoms shown by the 2 original plants in the field, and 33 plants of 5 descendent generations in the greenhouse were: prominent downward curling of many leaflets of each plant; diffuse mottling that often disappeared as the leaves matured; moderate chlorosis; dwarfing and severe brittleness of leaflets and stems; and yield reduced about 90 per cent (Fig. 4). The mottling and flavescence were often most prominent near the margins of the leaflets. The name, "curly flavescence," was given to it because the leaves were flavescent and prominently curled. Young leaflets were much curled but old leaves often showed only marginal curling. Curly flavescence was illustrated by Young and Morris (96). It was mentioned by Young (97).

Thirty-one normal Bliss Triumph potatoes were repeatedly inoculated at intervals of several days by transferring to each of them many aphids (*Myzus persicae* Sulz.) which had been colonized on plants showing curly flavescence. None of these plants nor 18 progeny plants from 9 of them developed symptoms of curly flavescence.

Eleven normal Bliss Triumph potato plants were repeatedly inoculated by transferring to them many aphids (*Macrosiphium solanifolii* Ashm., with some *Myzus persicae* Sulz.) which had been colonized on potato leaves with curly flavescence. None of these 11 parents nor 16 progeny plants from 10 of them developed symptoms of curly flavescence.

Leaves of curly-flavescence potatoes were used in leaf mutilation inoculations of 5 young normal Bliss Triumph potatoes. The inoculated plants developed no symptoms of curly flavescence.

Stems of 4 normal young Bliss Triumph potatoes were inarch grafted on 4 stems of curly-flavescence potatoes (separate plants). The inoculated plants developed no symptoms of curly flavescence.

*"Flavescence" was defined by Young and Morris (94). It is nonnecrotic chlorosis of organs that were not previously normally green.

Ten normal Bliss Triumph potato seed pieces were core grafted with cores from tubers with curly flavescence. These grafted seed pieces produced normal vines.

Since these attempts to transmit curly flavescence all failed, perhaps this is a genetic abnormality instead of a disease. If so, it may not be called mosaic.

Fig. 4.—Curly flavescence in a Bliss Triumph potato. Left—leaflets curled and dwarfed by curly flavescence; right—leaflets of a normal Bliss Triumph potato.

CURLY DWARF

Mottled curly dwarf appears to be caused by combined viruses of spindle tuber and mosaic. A selection of Green Mountain potatoes with spindle tuber showed typical, severe symptoms of curly dwarf in the progeny after infection of the parent vines with rugose mosaic in the field. Many Netted Gem potatoes with spindle tuber showed symptoms of curly dwarf after field infection with crinkle mosaic.

Many Bliss Triumph potatoes with mild symptoms of spindle tuber did not show typical symptoms of curly dwarf in the generation following infection with mosaic (probably mild mosaic) in the field.

LEAF ROLL

Three selections of Burbank potatoes (1924 crop) with severe leaf roll had unusual symptoms in the greenhouse. The plants were very small and spindly with light yellow, *downward curled* leaflets. The parents and other representatives of these selections had the usual leaf roll symptoms in the field.

As shown in Table 4, leaf roll was transmitted by stem and core grafts to 3 varieties of potatoes. Murphy and McKay (54) also transmitted leaf roll by core grafts. Six tomatoes inarch grafted on Netted Gem potato stems with leaf roll did not develop disease symptoms. Butler (15) reported the transmission of the leaf-roll virus to tomatoes, but said that the symptoms were often masked. Tuber cores separately containing the viruses of leaf roll and crinkle mosaic were placed in 4 potato seed pieces. Both diseases were transmitted to 1 potato plant, but only mosaic was transmitted in 3 other double grafts. Similar double inoculations with leaf roll and witches' broom transmitted only leaf roll in one case, and only witches' broom in another case.

A common symptom of leaf roll is the interveinal yellowing of the rolled leaves (Fig. 5 and Pl. 1, A). Young leaves are usually normally green. The interveinal yellowing is a plesionecrotic* symptom, and was described by Young and Morris (92). It was illustrated by Wortley (91). In late stages, brown, dead spots appear in the yellowed regions, which is evidence of the plesionecrotic nature of interveinal yellowing in leaf roll. This is not a constant symptom of leaf roll, but is common enough to be useful. Table 7 shows the effectiveness of roguing in the control of leaf roll.

*"Plesionecrotic symptoms" are those characteristic of the stages of relatively slow, necrotic, abnormal, protoplasmic degeneration preceding actual death of the cells. It occurs in organs that *were previously normally green* and often mature, so it is unlike flavescence which is a juvenile, nonnecrotic chlorosis (Young and Morris, 94). Yellowing and necrotic chlorosis are plesionecrotic symptoms. This term was proposed by Professor H. H. Whetzel, and is used with his permission.

In 1926 some otherwise normal Netted Gem potatoes in a field showed rolling and yellowing of the top leaves. Progeny from 10 of such plants were tested in the greenhouse. The seed

Fig. 5.—Leaf roll in a Bliss Triumph potato, showing the symptoms of interveinal yellowing and necrotic leaf spotting.

pieces from 8 of the plants developed at least 1 leaf-roll plant for each parent hill. The progeny of the other 2 hills were nearly normal. In 1927 an Irish Cobbler potato showed such primary symptoms. Two of its progeny had typical leaf roll. Hence, when the top leaves of a potato plant are chlorotic, rolled, and rather brittle late in the season, it indicates current season infection with some form of leaf roll. Hungerford and Raeder (40), Schultz and Folsom (67), and Murphy and McKay (54)

were among those who described these abnormalities as primary symptoms of leaf roll.

Cytological symptom: Triumph potato leaflets rolled and spotted by leaf roll were sectioned with a microtome. Many sections showed numerous intracellular, spherical or hemispherical bodies that appeared to be protoplasmic protuberances in many cases (Pl. 1, B). Most of these bodies were in or near the necrotic leaf spots killed by leaf roll and had diagnostic value. They stained red with Flemming's triple stain, and usually stained green with the Pianeze III B stain. Unstained sections of fresh material, cut in a block of ice on a microtome, showed the prominent yellow intracellular bodies. These bodies appeared to be effects and not causes of leaf roll. They may be similar to those described in stems by Artschwager (4). The tissues outside the necrotic leaf spots appeared to be nearly normal, but had the intracellular bodies near the leaf spots. The cells in these spots were collapsed, showing only a few layers of cells, so that the dead spots were only one-fourth as thick as the living parts of the leaves (Pl. 1, A). One necrotic region occupied only the lower part of the leaf (Pl. 1, C).

Folsom (28) described leaf roll. Tsen-Cheng (83) and Thung (81) studied physiological effects of leaf roll. Gilbert (32) correlated leaf roll and net necrosis of tubers. Smith (76) and Murphy and McKay (55) described insect transmission of leaf roll.

APICAL LEAF ROLL

Schultz and Bonde (71) described apical leaf roll as a new disease in the leaf roll group. The top leaves roll, resembling primary leaf roll, but this is the main symptom in tuber-perpetuated plants. Proof is lacking that this disease occurs in Montana.

LEAF ROLLING IN NORMAL POTATOES

Ten selections of normal Green Mountain potatoes and several selections of Green Mountain potatoes with mild and crinkle mosaics were planted in a field in 1926. The top leaves of most of the plants were prominently rolled and brittle but not distinctly chlorotic during the last two months of the growing

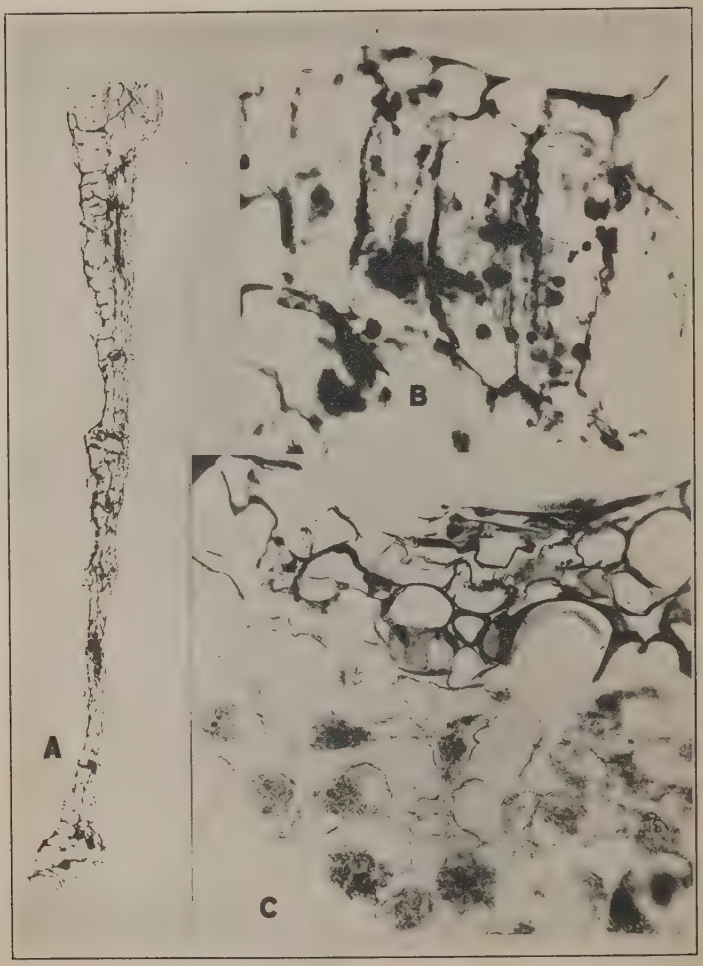

PLATE 1

A. Section of a necrotic leaf spot caused by leaf roll in a Bliss Triumph potato leaf. ×63.

B. Section of a Bliss Triumph potato leaf rolled by leaf roll, showing the intracellular globular bodies, some of which appear to be protoplasmic protuberances. ×522.

C. Section of a Bliss Triumph potato leaf rolled by leaf roll, showing a virus leaf spot that occupies only part of the leaf. Also a peculiar grouping of spherical bodies, supposedly chloroplasts, around nuclei. ×219.

season. These plants showed no other symptoms of leaf roll, and the progeny of those tested showed no symptom of leaf roll. Evidently this rolling of the top leaves was not a symptom of a disease.

The lower leaves of many potatoes, including normal ones, were commonly rolled and brittle when near or touching hot, dry soil, during five summers' observation. This was not interpreted as a symptom of a disease. Brown and silvery sheens appear sometimes on smooth potato leaves that are otherwise normal.

CALICO

Flavescent yellow or white irregular blotches 1 to 20 mm. wide constituted the usual leaf symptoms of calico (Fig. 6).

Fig. 6.—Calico in a Netted Gem potato. Parts of the leaves are yellowish-white in color.

Severely affected plants were dwarfed. Symptoms were more prominent in the field than in the greenhouse. With rare exceptions, calico was tuber perpetuated. It was studied in Triumph, Netted Gem, Pride, and Idaho Rural varieties.

Typically affected leaves were sectioned to see if abnormalities were present. No structural differences were seen, but this subject needs further study.

One potato planted in the greenhouse had an unusual symptom of calico. The Bliss Triumph parents had the usual symptoms in severe form in the field. The leaves of the progeny

Fig. 7.—Bliss Triumph potato leaf showing unusual symptoms of calico. The gray-white (hyaline) epiphyllous leaf spots are the only symptom.

(second generation) in the greenhouse lacked the large yellow blotchs in the leaves, but instead they had small, scattered, epiphyllous, hyaline blotches (Fig. 7). Sections through the hyaline blotches showed the morphological basis of this symptom. There were *no* palisade cells in the hyaline regions, which was quite unlike the condition found in leaves having the usual symptoms of calico.

Two tubers from this *second-generation* plant with the numerous hyaline blotches were planted in the greenhouse. The resulting vines showed *no* symptoms of calico in the *third generation.* This disappearance of calico is regarded as unusual.

Attempts were made to transmit calico to healthy potato plants. In 1926 and 1927, 22 seed pieces of Bliss Triumph, Green Mountain, and Irish Cobbler potatoes were core grafted with 2 selections of calico in Bliss Triumph potatoes. None of the grafted seed pieces produced plants with calico symptoms. Tubers from 7 of the plants were planted in the greenhouse later, but none of them produced plants with calico symptoms. Core grafting readily transmits several virus diseases of potatoes. Calico may be a genetic abnormality instead of a disease. Calico was described by Hungerford (39).

GIANT HILL

Giant hill was studied in Bliss Triumph and Netted Gem potatoes in the field. The vines were abnormally large and coarse, and bore irregular tubers that were cracked in many cases. Some selections of Triumph potatoes with giant hill were resistant to frost and *Alternaria solani* (E. and M.) J. and G. The symptoms of giant hill were masked in the greenhouse.

Triumph potatoes with giant hill were grown near other Triumph potatoes showing moderate or mild symptoms of spindle tuber at Bozeman in 1928 and 1929. The symptoms of these diseases were somewhat similar. Gilbert (31) discussed the similarities of these diseases. Dana (19) made core-graft inoculations with giant hill, and found giant hill symptoms in one inoculated plant.

Much work is needed to determine whether giant hill is a disease or a genetic abnormality.

SPINDLE TUBER

Severe cases of spindle tuber were diagnosed readily in the field, but many individual plants of Triumph selection No. 97 showed no recognizable vine symptoms for three years. However, the tubers of these plants and many other vines of this selection showed typical symptoms of spindle tuber. Narrowness of vines was a common, conspicuous symptom. Only severe cases were readily recognizable in the greenhouse.

One Netted Gem plant in the greenhouse showed the unusual spindle-tuber symptom of inverted leaflets, which was caused by a 180° twisting of some petioles.

Mild and severe forms of spindle tuber may represent only mild and severe cases of the disease, and not separate diseases. Some selections were more severely affected than others. Triumph selection No. 97 was rather mildly affected, and Gem selection No. 20 was severely affected during five years' observation.

Table 5 records transmission experiments with spindle tuber by core grafts in the field and the greenhouse. The symptoms were masked or absent in the greenhouse. Gem selection No. 20, used in the above experiments, was used in leaf-mutilation inoculations of 5 Triumph vines. None of the latter plants developed symptoms of spindle tuber.

Tables 9 and 10 show the reduction in yields caused by spindle tuber in Gem selection No. 20 and Triumph selection No. 97.

Folsom (29) and Werner (87, 88) are among those who published descriptions of spindle tuber. Goss (33) described important methods of transmitting spindle tuber. Goss (34, 35) reported transmissions by grasshoppers, flea beetles, tarnished plant bugs, and Colorado potato beetles.

Jones and Rawlins (45) used a new method of experimentation. They found that normal potato tissues and tubers usually had a higher resistance to electric current than diseased tissues and tubers.

UNMOTTLED CURLY DWARF

Observations for five years indicated that unmottled curly dwarf is distinct from spindle tuber. Two selections of Earliest-

of-all potatoes showed extreme symptoms of unmottled curly dwarf. Their leaflets were extremely downward curled and very rugose. The vines were upright, very narrow, dark green, and only 10 to 35 cm. tall. The tubers were smooth and only 1 to 2 cm. in diameter.

Triumph selection No. 101 showed symptoms of unmottled curly dwarf in less extreme and more typical form. Table 5 records transmissions by core grafts. The parents of the diseased cores (scions) had dwarfed, narrow tops with dwarfed, often rugose, sometimes curled leaflets, and dwarfed, often cracked tubers. Tubers produced in fields were not elongate with too many eyes, thus lacking symptoms of spindle tuber. Some new tubers in the greenhouse were oblong, irregular, and had deeply depressed eyes when they were only 1 cm. long.

A necrotic symptom appeared in this selection in 1929. Tubers grown in a dry field and in a greenhouse bore depressed, corky, brown, usually cracked lesions 5 to 10 mm. wide, besides the common deep cracks. Sections revealed no foreign organisms associated with the corky lesions, but showed peculiar clusters of small starch grains in the tuber tissues near the corky layers. These brown lesions bore some resemblance to those illustrated in Plate IV by Quanjer (60).

Burr (14) gave evidence that unmottled curly dwarf is distinct from spindle tuber, and mentioned internal necrosis of tubers as a current season symptom following inoculation of tops.

PSYLLID YELLOWS

Psyllid yellows appeared in an experimental plot at Bozeman in August, 1927, when some Irish Cobbler and Burbank potato vines showed symptoms of this disease. Psyllids were collected from the affected plants by W. L. Jellison. Tubers from affected plants were planted in the greenhouse. None of the resulting vines had psyllid yellows.

Richards (63) described psyllid yellows. Binkley (8) said that it was not transmitted by non-viruliferous psyllids reared from eggs under controlled conditions. He transmitted psyllid yellows with viruliferous psyllids. This evidence showed that it is a virus disease. Shapovalov (73) said that psyllid yellows was tuber perpetuated in some cases.

WITCHES' BROOM

Recent experiments showed that the underground tubers produced by potatoes with secondary symptoms of witches' broom had a long dormant period when they were not sprouted at digging time. Tubers borne on vines with secondary witches' broom usually did not sprout in the field under ordinary conditions. Ten Jersey Peachblow tubers from vines showing prominent secondary symptoms of witches' broom were stored in a refrigerator for one week immediately after digging, and then they were planted in sand. Sprouts appeared on 2 of the tubers in 58 days, and on the other 8 tubers within 65 days after planting.

Later, 20 Bliss Triumph potato tubers from vines showing prominent secondary symptoms of witches' broom were stored in the refrigerator for 69 days immediately after digging, and then they were planted in sand. Many healthy Bliss Triumph potatoes were stored for a month or 6 weeks after digging, and then were planted with the above diseased tubers. Most of the witches' broom and normal potatoes produced leaves in about 40 days. Tubers with witches' broom from the 1929 crop were stored in a refrigerator for 5 months. When planted, they required more than 50 days to produce leaves, while corresponding normal tubers bore leaves within 20 days.

The dormancy of some tubers on plants with primary symptoms of witches' broom was often abnormally short because they sprouted late in the summer, forming many little stems at the base of the parent vines. Successive generations of potatoes with secondary witches' broom occurred at intervals of about 60 days in the greenhouse. Hence, there was a short period of dormancy in some cases, but not in others. There was some evidence of secondary dormancy in which sprouts appeared to be dormant for a few weeks. The appearance of leaves on aerial tubers did not mean broken dormancy.

Attempted transmissions by aphids: Some tests using *Myzus persicae* Sulz. were reported by Young and Morris (94, p. 846). Normal Bliss Triumph potatoes 6 to 20 cm. tall were inoculated in the following greenhouse experiments not previously described.

Many individuals of *Myzus persicae* Sulz. from potatoes with secondary witches' broom were repeatedly transferred to 24 healthy potato plants. Eighteen progeny plants from 8 of these parents were later grown in the greenhouse. None of these 42 plants developed definite symptoms of witches' broom.

Many individuals of *Macrosiphum solanifolii* Ashm. from potatoes with witches' broom were repeatedly transferred to 14 healthy potato plants. Ten progeny from 8 of these parents were later grown in the greenhouse. Some individuals of *Myzus persicae* were mixed with those of *Macrosiphum*. None of these 24 plants developed definite symptoms of witches' broom. All of these and previous attempts failed to transmit witches' broom by means of aphids. Table 6 gives transmissions of witches' broom in a field. Part of the information in it was previously reported.

Evidence from five years' observation suggested that witches' broom occurred in two degrees of severity. Triumph selection No. 115 and one hill of Cobbler selection No. 620, both having witches' broom, produced vines of normal size when tubers weighing 30 to 100 grams were planted. Many of the stems showed no symptoms of witches' broom. The other selections of potatoes, like Triumph selection No. 144, did not produce tubers weighing 30 to 60 grams, so had less chance to produce large vines. Selections No. 115 and No. 144 differed mainly in the sizes of the vines and tubers that they produced.

Combinations of crinkle mosaic and witches' broom may be separated by leaf-mutilation inoculation, which is known to transmit only the crinkle mosaic. Young (93, 95) and Young and Morris (92, 94) described transmissions of witches' broom from diseased potatoes to healthy potato, tomato, and tobacco plants. Unlike rugose mosaic, witches' broom usually caused primary symptoms when inoculated by core grafts. Hungerford and Dana (41) gave the first good description of witches' broom. Dana (18) reported apparent transmission of witches' broom. Holmes (37) studied witches' broom with ultra-violet light.

STUDY OF SECTIONS OF BUDS

Sections stained with Flemming's triple stain were made of normal potato buds, and of buds on potato stems diseased with witches' broom, witches' broom and crinkle mosaic in combination, unmottled curly dwarf, spindle tuber, and rugose mosaic, in six varieties of potatoes.

Study of the sections revealed no apparent differences in mitosis or structure between the buds from the normal and the diseased potato stems. The negative results in these preliminary studies are inconclusive, but indicate a promising line of investigation.

Schaffnit and Weber (66) mentioned intracellular bodies associated with the growing points of plants affected with mosaic.

SPINDLING SPROUT

Spindling sprout is a symptom and not a separate disease. It is a symptom of witches' broom (Young and Morris, 92, 94).

Many normal potatoes of a few varieties were stored for one-year periods in a refrigerator at 0° to 10° C. They developed spindling sprouts in storage and after planting. This was especially noticeable on the tubers that had secondary tubers on their sprouts. This form of spindling sprout was observed from 1926 to 1930. Spindling sprout, resulting from long cold storage, was less severe than that caused by witches' broom. Decay of seed pieces while sprouts were forming also caused spindling sprouts.

Schultz and Folsom (67) gave net necrosis and spindling sprout as symptoms of leaf roll. Gilbert (32) correlated leaf roll and net necrosis.

ATTEMPTED TRANSMISSION OF WITCHES' BROOM TO SUGAR BEETS

Three series of inoculations were made to try to transmit witches' broom of potatoes to normal sugar beets by core grafts. Cores 1 cm. in diameter were cut from potatoes and placed in holes made in sugar-beet roots. The sugar beets were 2 to 10 cm. in diameter. Eyes were left on the ends of many of the potato cores. After grafting, the beets were planted in the

greenhouse for a few months. Twenty-five of these potato-beet grafts were made. The cores rotted in 13 of the beets.

Potato sprouts grew from the eyes of 12 of the cores in the beets. The sprouts became 5 to 10 cm. tall and bore leaves and a few roots. Their cores were firmly attached to the beets, and enlarged till their ends protruded 5 mm. beyond the holes in the beet roots. These cores and sprouts remained alive for 28 to 40 days.

Of the potato cores that grew, 10 came from Bliss Triumph and Jersey Peachblow potatoes having severe witches' broom, and 2 came from normal Bliss Triumph potatoes. The graft calluses were brown as they were in grafts of herbaceous stems.

The sugar beets grew for a few months after grafting. Two of them, containing potato cores with witches' broom, developed a peculiar white blotching in the beet leaves.

Three of the sugar beets, grafted with cores of witches'-broom potatoes, were grown in the greenhouse for two months and were then stored in a refrigerator during one summer. When returned to the greenhouse in the fall, large numbers of small leaves appeared on the sides of their crowns, possibly because the tops of the crowns developed poorly. They did not produce seed stalks.

Although these abnormalities in the sugar beets were very interesting, they were too indefinite to justify conclusions.

EFFECT OF VIROSES ON THE STARCH CONTENT OF POTATO STEMS

The stems of many potatoes were microscopically examined, and treated with strong iodine to see whether the presence of stored starch had diagnostic value in recognizing virus diseases. Much of the stem starch seen differed from tuber starch in that the grains were nearly spherical with a few lines radiating from the centers, rather than elongate with excentric, concentric striae like tuber starch (Young and Morris, 94). These stem-starch grains were much smaller than most tuber-starch grains. Stem-starch grains were 3 to 8 microns in diameter, and occurred singly or in groups of 2 to 5. Potato stems affected separately with witches' broom, spindle tuber, unmottled curly dwarf, and leaf roll contained many small grains of the stem-starch type.

Some starch was found in potato stems affected with leaf rolling mosaic. Most of the normal potato stems and those affected with mild mosaic contained little or no stored starch.

Useful tests were made by slicing off the epidermal, and part of the cortical, layers of potato stems, and painting the wounds with concentrated iodine. Abundant starch was quickly indicated by blackening.

Abundant grains of the tuber-starch type were seen in some stems separately affected with leaf roll, rugose mosaic, and spindle tuber. Stored starch (usually the stem-starch type) was abundant in some normal potato stems, so the presence of abundant starch in stems was usually, but not always, a symptom of viroses.

WEED AND CULTIVATED HOSTS OF POTATO VIRUSES

Weed and cultivated hosts of potato viruses deserve increasing attention. *Solanum triflorum* Nutt., *S. douglasii* Dunal., *S. rostratum* Dunal., and *Hyoscyamus niger* L. occur in Bozeman. *Physalis heterophylla* Nees, *P. lanceolata* Michx., *P. longifolia* Nutt., and *Solanum nigrum* L. have been collected in Montana. Species of cultivated solanaceous plants may harbor some viruses of potatoes. Schultz and Folsom (68) transmitted mild mosaic of potato to *Solanum nigrum* L. Dana (19) and Valleau (84) mentioned weed hosts. Smith (77) made interspecific transmissions. He (75) found that potato mosaic increased in virulence when it passed through tobacco.

Annual hosts are less important than perennial hosts. Practically, the potato is a perennial host because viruses are carried in the underground stems (tubers).

EXPERIMENTS IN ROGUING

Seed stocks of potatoes containing large percentages of tubers with virus diseases were prepared by erratically mixing diseased tubers and seed pieces with mostly normal check tubers and seed pieces. The seed pieces were planted 50 cm. apart in rows that were 90 cm. apart. This wide spacing facilitated roguing.

Tables 7 and 8 give the results of these experiments. Three kinds of plots were used. (a) The potatoes were planted in

4-hill units of either normal or diseased tubers. Many of the 4-hill units were tuber units when the tubers were large enough. Seed pieces were cut and planted on the same day. (b) Single (numbered) hills. The 800 seed pieces for each plot were cut one or two months before planting, and were stored in a refrigerator. They were numbered consecutively with India ink or indelible pencil. Such numbers remained legible for one to three months after planting. Three seed pieces were cut from each tuber, each piece bearing the same number. A piece of each tuber was planted in Montana, Oregon, and Utah.* Subsequent comparison of notes gave comparisons on roguing and symptoms in different localities. (c) Single hills were distributed in the ordinary form of mass planting. The seed pieces were mixed in boxes before planting. They were cut and planted on the same day.

Each plot was rogued carefully at intervals of about ten days, beginning as soon as disease symptoms were readily distinguishable and continuing until the hills were dug. The four plots each year were planted in the same small field.

Methods were improved in 1929 when planting records were kept. The numbers of the hills and units known to be diseased were recorded in the office. After frost had killed all of the potato vines, the planting records were (for the first and only time) taken to the plots and checked against the hills remaining in the plots. All of the added hills from known diseased parents that had been missed in roguing were now dug separately. Indices of these separately dug Triumph hills were planted in the greenhouse, and indices of the Gem hills were planted in the field to determine why they were missed in roguing. Crinkle mosaic was diagnosed in indices from each of the Triumph hills and the Triumph tuber-unit missed in roguing and dug separately.

Without impairing the value of the experiment, this use of the planting records saved one season's work in showing the effectiveness of the roguing. The planting records on the num-

*This was a cooperative project involving the Agricultural Experiment Stations of Montana, Oregon, and Utah, and the United States Department of Agriculture. The potatoes used in 1927 were sent from Oregon by Dr. M. B. McKay and Mr. T. P. Dykstra. The potatoes used in 1929 and 1930 were supplied by Dr. P. A. Young and Professor H. E. Morris.

bered hills were sent to Oregon and Utah on September 11, 1929, so that they could be used similarly there.

Tubers that did not produce aerial stems were not considered in the tables.

Table 8 gives two sets of percentages: the percentage of the added diseased plants that were rogued, and the total percentage of diseased plants that were rogued.

Progeny of the unrogued check hills from the 1929 plots were planted in 1930 to see if diseases spread to them.

The results presented in Tables 7 and 8 show that roguing was effective in reducing the viroses to low percentages.

REDUCTIONS IN YIELD CAUSED BY VIRUS DISEASES

Experimental plots of potatoes were planted at Bozeman, Montana, in 1927, 1928, and 1929, to determine the reductions in yield caused by mosaic diseases and spindle tuber. Preliminary results were given by Morris and Young (51).

The figures given in Tables 9 and 10 indicating reductions in yield represent the reductions caused by 100 per cent infestations of the diseases in all cases.

The potatoes were planted in alternating groups of 4 diseased and 4 healthy hills, many of which groups represented tuber units when the tubers were sufficiently large. The natures of the units were recorded by symbols such as $1–^{4}$, $2–^{2}$, $4–^{0}$, etc., signifying one tuber quartered, two tubers cut in halves, and four tubers planted whole. Only one seed piece was planted in each hill.

In Tables 9 and 10, Triumph selections No. 97 and No. 112 usually produced tubers weighing only 20 to 120 grams each. All of the other stocks of potatoes usually produced tubers weighing 50 to 500 grams each, so the seed pieces of Idaho Rural selection No. 44 and Gem selection No. 86 averaged as heavy as their check seed pieces in the plots. In many cases, the seed pieces of Nos. 20, 97, and 112 were smaller than the corresponding check seed pieces. The comparative effects of the small seed pieces (20 to 50 grams) on yields reflected the effects of their diseases, so they were properly expressed in the reductions in yields.

The potatoes were planted 50 cm. apart in rows that were 90 cm. apart. The wide spacing in the rows reduced the effects of the hills on each other (Stewart, 79). The hills were planted at the rate of 8712 hills per acre.

Check vines showing diseases and diseased-stock vines showing combination diseases were rogued. They were not considered in the tables. This necessary roguing was done to eliminate diseases arising from the small amount of annual spread of diseases in the fields, because the diseased and healthy plants grew in the same plots. The plots were not irrigated, but received a little subirrigation water. Young (97) gave conclusions from these experiments, using averages weighted on the basis of the total numbers of hills. Tables 9 and 10 give better interpretations without weighting the averages by the total numbers of hills, although the two methods give only small differences in average percentages.

The yields per acre and the reductions in yields were calculated from the totals of the hills and yields for each group. The following formula and example show the method of calculation.

$$\frac{\text{Yield (pounds)}}{\text{Number of hills}} \times \frac{8712 \text{ (hills per acre)}}{60 \text{ (pounds per bushel)}} = \text{bushels per acre.}$$

$$\text{Example: } \frac{194}{91} \times \frac{8712}{60} = 309.5 \text{ bushels per acre.}$$

Folsom, Schultz and Bonde (30), Wedgworth (86), Krantz and Bisby (4), and Morris and Young (51, 52) are among those who published data on reductions in yields caused by viroses. Such data are needed for different regions.

SUMMARY

Willowy, spindling tops are a late-season symptom of rugose mosaic and crinkle mosaic in greenhouses.

By leaf-mutilation inoculations and tuber-core grafts, rugose mosaic was transmitted from potatoes to other potatoes 75 times in 127 trials.

By leaf-mutilation inoculations rugose mosaic was transmitted from potatoes to tobacco and tomato plants 10 times in 14 trials, causing mottling in them.

The incubation period for rugose mosaic was usually 21 to 40 days.

The rugose-mosaic virus was transmitted to potatoes separately containing the viruses of mild mosaic, leaf rolling mosaic, and spindle tuber. Symptoms of rugose mosaic appeared prominently in them in addition to the symptoms of the viroses which they had before the inoculations. These results constitute additional evidence that the four viruses are different.

The rugose-mosaic virus did not cause primary symptoms, nor alter any symptoms when it was inoculated by leaf-mutilation inoculations into potatoes already having secondary symptoms of rugose mosaic.

Necrotic leaf spots are an important symptom of rugose mosaic.

Heavy infestations of non-viruliferous individuals of *Macrosiphum solanifolii* caused brown dots and general browning of the veins of normal potato leaflets.

Heavy infestations of non-viruliferous individuals of *Myzus persicae* caused dwarfed, spindly tops and dwarfed, curled leaflets of normal potatoes.

All normal seed pieces core grafted with cores from healthy tubers produced healthy potatoes.

Leaf rolling mosaic, super-mild mosaic, mild mosaic, spindle tuber, unmottled curly dwarf, witches' broom, and leaf roll were transmitted by core grafts.

Globular, intracellular bodies in brittle, rolled leaves had diagnostic value in leaf roll.

Interveinal yellowing was a common symptom of leaf roll.

Super-mild mosaic reduced yields 19.1 per cent, although dim mottling was the only evident aerial symptom.

Curly flavescence was not transmitted in any of the many trials, so it may be a genetic abnormality.

Calico was not transmitted in any of the 22 core grafts. It may be a genetic abnormality.

Two distinct sets of symptoms of calico occurred in one selection of Bliss Triumph potatoes. No palisade cells were developed in the epiphyllous hyaline spots in the leaves of one plant. Descendent plants had no symptoms.

Unmottled curly dwarf seemed to be a distinct disease. It was transmitted to normal potatoes.

Depressed, brown, cracked, corky lesions in tubers were symptoms of unmottled curly dwarf in tubers.

Normal dormancy was common in tubers produced by vines with secondary symptoms of witches' broom. Short dormancy periods occurred under other conditions.

Cores of potatoes placed in sugar-beet roots probably failed to transmit witches' broom to sugar beets, although graft unions occurred, the cores grew, potato stems and roots grew from the sides of the sugar-beet roots, and odd symptoms appeared in the beet leaves.

Roguing was very effective in eliminating crinkle mosaic, leaf roll, and spindle tuber from seed stocks.

Reductions in yields varying from 19 to 75 per cent caused by spindle tuber, crinkle mosaic, mild mosaic, and super-mild mosaic, were determined in yield plots.

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TABLE 1.—FIELD TRANSMISSION OF RUGOSE MOSAIC BY APHIDS IN 1926

Variety	Primary symptoms	Tubers tested from 1 hill	Number with mosaic	Number healthy
Bliss Triumph	Severe	6	6	0
Bliss Triumph	Trace	4	0	4
Bliss Triumph	Severe	5	5	0
Bliss Triumph	Severe	8	8	0
Bliss Triumph	Severe	10	10	0
Irish Cobbler	Severe	4	4	0
Earliest-of-all	Moderate	9	3	6
Green Mountain	Moderate	12	12	0
Green Mountain	Severe	4	*4	0
Green Mountain	Severe	4	*4	0
Netted Gem	Mild	8	7	1
Netted Gem	Mild	3	3	0
Idaho Rural	Moderate	8	8	**0

*These hills had spindle tuber before infection with rugose mosaic.
**1927 seed; the rest was 1926 seed.

TABLE 2.—TRANSMISSION OF MOSAIC FROM DISEASED TO HEALTHY POTATOES IN 1926 AND 1927

Variety of potatoes with inoculum	Disease in inoculum	Variety of inoculated potatoes	No. of inoculations	No. successful	Type of inoculations	Healthy checks from same tubers
Green Mountain	Leaf rolling mosaic	B. Triumph	2	2	Core graft	2
Green Mountain	Leaf rolling mosaic	Netted Gem	2	1	Core graft	3
Idaho Rural	Mild mosaic	B. Triumph	4	3	Core graft	1
Idaho Rural	Mild mosaic	I. Cobbler	2	0	Core graft	1
Idaho Rural	Mild mosaic	Netted Gem	2	0	Core graft	2
Bliss Triumph	Mild mosaic	Gr. Mountain	1	1	Core graft	2
Bliss Triumph	Mild mosaic	B. Triumph	11	6	Core graft	12
Bliss Triumph	Mild mosaic	B. Triumph	20	2	Leaf mutilation	18
Bliss Triumph	Mild mosaic	B. Triumph	10	0	Stem graft	many
Bliss Triumph	Mild mosaic	B. Triumph	9	2	Core graft	4
Bliss Triumph	Crinkle mosaic	I. Cobbler	2	0	Core graft	2
Bliss Triumph	Crinkle mosaic	Netted Gem	5	4	Leaf mutilation	4
Bliss Triumph	Crinkle mosaic	J. Peachblow	1	0	Leaf mutilation	3
Bliss Triumph	Rugose mosaic	B. Triumph	4	2	Leaf mutilation	1
Bliss Triumph	Crinkle mosaic	Rural N. Yorker	3	0	Core graft	1
Bliss Triumph	Crinkle mosaic	I. Cobbler	1	0	Tuber smear	
Bliss Triumph	Crinkle mosaic	I. Cobbler	2	0	Tuber soak	
Bliss Triumph	Crinkle mosaic	Netted Gem	4	0	Tuber smear	3
Bliss Triumph	Crinkle mosaic	Netted Gem	4	0	Tuber soak	3
Bliss Triumph	Crinkle mosaic	B. Triumph	2	0	Tuber soak	2
Jersey Peachblow	Crinkle mosaic	B. Triumph	11	5	Leaf mutilation	many
Jersey Peachblow	Crinkle mosaic	Netted Gem	5	0	Leaf mutilation	5
Netted Gem	Super-mild mosaic	B. Triumph	2	0	Stem graft	many
Netted Gem	Super-mild mosaic	B. Triumph	8	5	Core graft	9
Netted Gem	Super-mild mosaic	B. Triumph	4	0	Core graft	4

TABLE 3.—TRANSMISSION OF VIRUSES TO POTATOES ALREADY CONTAINING ONE VIRUS

Variety of potatoes with inoculum	Disease in inoculum	Variety of inoculated potatoes	Disease in inoculated potatoes	No. of inoculations	No. successful	Type of inoculation	Checks	Incubation period (days)
Bliss Triumph	Rugose mosaic	I. Cobbler	Mild mosaic	6	1	Core graft	4	33
Bliss Triumph	Crinkle mosaic	J. Peachblow	Crinkle mosaic	2	0	Core graft	1	
Bliss Triumph	Rugose mosaic	B. Triumph	Spindle Tuber	2	1	Core graft	2	34
Irish Cobbler	Rugose mosaic	J. Peachblow	Crinkle mosaic	1	0	Core graft	0	
Irish Cobbler	Rugose mosaic	Netted Gem	Mild mosaic	3	2	Core graft	2	33–57
Irish Cobbler	Rugose mosaic	Gr. Mountain	Lf. roll. mosaic	1	1	Aphids	4	about 30
Irish Cobbler	Rugose mosaic	Gr. Mountain	Lf. roll. mosaic	4	1	Lf. mutilation	1	15
Irish Cobbler	Rugose mosaic	Bliss Triumph	Rugose mosaic	10	0	Lf. mutilation	13	

TABLE 4.—TRANSMISSIONS OF POTATO LEAF ROLL IN 1926

Variety of potatoes with inoculum	Variety of inoculated potatoes	No. of inoculations	No. of infections	Type of inoculation	Incubation period in days	Healthy checks from same tubers
Bliss Triumph	Bliss Triumph	13	9	Core graft	48–52	11
Bliss Triumph	Idaho Rural	1	1	Core graft	42	1
Bliss Triumph	Netted Gem	2	0	Core graft	....	5
Bliss Triumph	Rural New Yorker	2	0	Core graft	....	2
Bliss Triumph	Bliss Triumph	2	1	Stem graft	48	many
Burbank	Bliss Triumph	2	0	Stem graft	....	0
Burbank	Bliss Triumph	9	0	Lf. mutilation	....	many
Burbank	Bliss Triumph	8	3	Core graft	47–69	many
Bliss Triumph	Irish Cobbler	6	3	Core graft	48–70	6

TABLE 5.—CORE GRAFTS OF TUBERS TO TRANSMIT UNMOTTLED CURLY DWARF AND SPINDLE TUBER

Variety of potatoes with inoculum	Disease in inoculum	Variety inoculated	Where planted	No. of plants inoculated	No. of plants infected	Checks
Triumph	Unmottled curly dwarf	Triumph	Field*	14	8	*6
Triumph	Unmottled curly dwarf	Netted Gem	Field	10	1	*10
Netted Gem	Spindle tuber	Netted Gem	Field	12	0	*9
Netted Gem	Spindle tuber	Triumph	Field	3	0	*2
Green Mountain	Spindle tuber	Triumph	Field	8	5	*4
Triumph	Spindle tuber	Triumph	Field	9	4	*4
Triumph	Spindle tuber	Netted Gem	Field	4	0	*2
Netted Gem	Spindle tuber	Triumph	Greenhouse	5	0	3
Netted Gem	Spindle tuber	Cobbler	Greenhouse	4	1	4

*These checks came from the same tubers as the core-grafted seed pieces.
**Field experiments were in 1928; greenhouse experiments were in 1926.

TABLE 6.—TRANSMISSION OF WITCHES' BROOM BY CORE GRAFTS IN FIELD IN 1927

Variety of potatoes with inoculum	Variety of potatoes inoculated	Number of inoculations	Number successful	Healthy checks from same tubers
Jersey Peachblow	Irish Cobbler	9	4	8
Jersey Peachblow	Idaho Rural	6	4	6
Bliss Triumph	Bliss Triumph	14	4	9
Total		29	12	23

TABLE 7.—ROGUING CRINKLE MOSAIC AND LEAF ROLL FROM POTATO PLOTS IN 1927 AND 1928

Variety	Disease predominating	1927				1928		
		How planted	Number of hills in plot	Number removed*	Per cent removed	How planted	Number of hills in plot**	Per cent removed and disease
Burbank	Crinkle mosaic	Numbered single hills	800	196	24.5	Single hills	416	0.24 mosaic
Burbank	Crinkle mosaic	Unnumbered single hills	871	191	21.9	4-hill units	740	0.54 mosaic
Netted Gem	Leaf roll	Numbered single hills	800	190	23.8	Single hills	468	0.2 mosaic 0.2 leaf roll
Netted Gem	Leaf roll	Unnumbered single hills	917	168	18.3	4-hill units	744	2.7 leaf roll 1.6 mosaic

*5 to 10 plants with other virus diseases were rogued from each plot. These were disregarded here.
**Seed pieces for these four plots were taken from the plots of numbered hills grown in 1927.

TABLE 8.—ROGUING CRINKLE MOSAIC AND SPINDLE TUBER FROM POTATO PLOTS IN 1929

Variety	How planted	Disease in tubers added	No. of hills in plot	Diseased hills added to seed stock and intermingled with the checks			Checks hills removed*	Per cent of total hills removed
				Number added	Number removed	Per cent removed		
Triumph	4-hill units	Crinkle mosaic	840	248	244	98.4	44	34.3
Triumph	Single hills	Crinkle mosaic	**685	202	199	98.5	128	47.7
Netted Gem	4-hill units	Spindle tuber	840	208	204	98.1	32	28.1
Netted Gem	Single hills	Spindle tuber	**769	183	176	96.2	101	36.0

*These hills, planted as checks, were rogued because they showed symptoms of diseases.
**800 hills were planted, but the ones that did not produce leaves were disregarded.

TABLE 9.—REDUCTIONS IN YIELDS OF POTATOES CAUSED BY VIRUS DISEASES

Selection No. and variety	Disease	Year	Number of hills	Yield in pounds	Calculated yield in bus. per acre	Per cent reduction in yield
34. Bliss Triumph	Normal	*1927	91	194	309.5	
Bliss Triumph	Normal	**1927	88	239.5	395.2	
Bliss Triumph	Normal	1928	177	605	496.3	
Bliss Triumph	Normal	1929	200	506	367.4	
Average					392.1	
97. Bliss Triumph	Spindle Tuber	**1927	114	144.5	184.1	53.4
Bliss Triumph	Spindle Tuber	1928	179	310	251.4	49.4
Bliss Triumph	Spindle Tuber	1929	58	95	237.8	35.3
Average					224.4	42.8
112. Bliss Triumph	Crinkle mosaic	*1927	139	195	203.7	34.2
Bliss Triumph	Crinkle mosaic	1928	270	463	249.0	49.8
Bliss Triumph	Crinkle mosaic	1929	99	159	233.2	36.5
Average					228.6	41.7
81. Irish Cobbler	Normal	1928	87	333.5	556.6	
402. Irish Cobbler	Spindle tuber	1928	108	229	307.8	44.7

*The units of normal hills were mixed with those diseased with crinkle mosaic.
**The units of normal hills were mixed with those diseased with spindle tuber.

TABLE 10.—REDUCTIONS IN YIELDS OF POTATOES CAUSED BY VIRUS DISEASES

Selection No. and variety	Disease	Year	Number of hills	Yield in pounds	Calculated yield in bus. per acre	Per cent reduction in yield
31. Netted Gem	Normal	1927	91	216	344.7	
Netted Gem	Normal	1928	163	658.5	586.6	
Netted Gem	Normal	1929	200	642	466.1	
Average					465.8	
20. Netted Gem	Spindle tuber	1927	89	51	83.2	75.9
Netted Gem	Spindle tuber	1928	185	307.5	241.3	58.9
Netted Gem	Spindle tuber	1929	88	74	122.1	73.8
Average					148.9	68.0
86. Netted Gem	Super-mild mosaic	1928	67	227.5	493.0	16.0
Netted Gem	Super-mild mosaic	1929	100	247	358.6	23.1
Average					425.8	*19.1
389. Idaho Rural	Normal	1928	62	191.5	448.5	
Idaho Rural	Normal	1929	96	209	316.1	
Average					382.3	
44. Idaho Rural**	Mild mosaic	1928	95	218	333.2	25.7
Idaho Rural	Mild mosaic	1929	100	175.5	254.8	19.4
Average					294.0	23.1

*Netted Gem checks in 1928 and 1929 had an average yield of 526.3 bu. per A. This variety is also called Russet Burbank.

**Mottling and ruffling of the leaves were constant symptoms.